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A CONTRIBUTION TO THE SYSTEMATICS OF THE REPTILIAN MALARIA PARASITES, FAMILY PLASMODIIDAE (APICOMPLEXA: HAEMOSPORORINA)

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A CONTRIBUTION TO THE SYSTEMATICS OF THE REPTILIAN MALARIA PARASITES, FAMILY PLASMODIIDAE (APICOMPLEXA: HAEMOSPORORINA).

Sam Rountree Telford, Jr.*

ABSTRACT

The malaria parasites of reptiles, represented by over 80 known species, belong to three genera of the Plasmodiidae: *Plasmodium*, *Fallisia*, and *Saurocytozoon*. *Plasmodium*, containing most of the species, is comprised of seven subgenera: *Sauramoeba*, *Carinamoeba*, *Lacertamoeba*, *Paraplasmodium*, *Asiamoeba*, *Garnia*, and *Ophidiella*. Of these, *Lacertamoeba*, *Paraplasmodium*, and *Asiamoeba* are new subgenera. The subgenera are defined on the basis of morphometric relationships of the pigmented species, by the absence of pigment (*Garnia*), or by their presence in ophidian hosts (*Ophidiella*). The pigmented species with schizonts and gametocytes of similar size are divided into three groups with little or no morphometric overlap: *Sauramoeba*, with very large gametocytes and schizonts, which undergo 4 to 7 nuclear divisions in the erythrocytic phase of the life cycle; *Carinamoeba*, with very small gametocytes and schizonts, that have 2 or 3 divisions; and *Lacertamoeba*, with medium-sized gametocytes and schizonts, which undergo 3 to 5 nuclear divisions. *Lacertamoeba* species that overlap morphometrically with *Carinamoeba* can be distinguished from the latter by their larger range of merozoite numbers. Two species groups have schizonts and gametocytes of dissimilar size: *Paraplasmodium* has large gametocytes but schizonts of only medium size, while *Asiamoeba* has gametocytes 4 to 15 times the schizont size. *Paraplasmodium* is further distinguished by containing the only species known to undergo normal sporogony in a psychodid fly (*Lutzomyia*), and by its capacity to produce exoerythrocytic schizonts in both fixed and wandering host cells. *Fallisia* is characterized by having both asexual and sexual cycles in non-erythrocytic blood cells, while the asexual stages of *Saurocytozoon* appear to be transitory in circulating lymphocytes, disappearing when gametocytes, largely confined to lymphocytes, become evident.

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RESUMEN

Los parásitos tipo malaria de los reptiles, representados por más que 80 especies conocidas, se clasifican en tres géneros de la familia Plasmodiidae: *Plasmodium*, *Fallisia*, y *Saurocytozoon*. *Plasmodium* contiene la mayor parte de las especies, y se divide en 7 subgeneros: *Sauramoeba*, *Carinamoeba*, *Lacertamoeba*, *Paraplasmodium*, *Asiamoeba*, *Garnia*, y *Ophidiella*. De estos subgéneros, *Lacertamoeba*, *Paraplasmodium*, y *Asiamoeba* son nuevos. Los subgéneros se definen por los relaciones morphométricas en las especies pigmentados, por la absencia de hemozoina (*Garnia*), o por su presencia en hospederos ofidios (*Ophidiella*). Las especies pigmentadas con esquizontes y gametocitos de tamaños similares se separan en tres grupos nítidos: *Sauramoeba* tiene los gametocitos y esquizontes muy grandes, y éstos tienen 4 a 7 divisiones nucleares en la fase eritrocítica del ciclo de vida; *Carinamoeba*, con los gametocitos y esquizontes muy pequeños, con 2 a 3 divisiones nucleares; y *Lacertamoeba* con los gametocitos y esquizontes de tamaño medio, con 3 a 5 divisiones nucleares. Las especies de *Lacertamoeba* que se parecen morfológicamente a *Carinamoeba* se pueden distinguir del último por la mayor variación en los números de merozoitos. Dos grupos de especies tienen esquizontes y gametocitos de tamaños desiguales: *Paraplasmodium* tiene los gametocitos muy grandes y los esquyizontes de tamaño medio, mientras que *Asiamoeba* tiene gametocitos de 4 a 15 veces mayores que los esquizontes. *Paraplasmodium* se distingue además por contener la única especie de *Plasmodium* conocida en que la esporogonia sucede en una mosca psicódida (*Lutzomyia*), y por la capacidad de producir esquizontes exoeritrocíticas tanto en la células hospederas fijas como en las errantes. *Fallisia* se caracteriza por tener ambos ciclos, asexual y sexual, en células de sangre no-eritrocíticas, mientras que los esquizontes de *Saurocytozoon* parecen ser transitorias en linfocitos, pues desaparecen cuando hay gametocitos, estos principalmente limitados a los linfocitos.

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INTRODUCTION

The malarial parasites of lizards were placed by Garnham (1966) into two subgenera of *Plasmodium*, *Carinamoeba* and *Sauramoeba*, which were distinguished by size of erythrocytic schizonts alone. The only definition of the two groups was that *Sauramoeba* had "large" schizonts while those of *Carinamoeba* were "small." This did not provide a clear criterion for separation of the species, but given the lack of precision characteristic of most taxonomic descriptions of saurian malarias up to that time (Telford, 1973), this was perhaps the only separation possible. Telford and Ball (1969) supposedly quoted Garnham as limiting *Carinamoeba* to those forms with a "maximum of 12 merozoites," citing his comment on page 819 as authority for this limitation. Viewed in retrospect, this passage probably referred to *Plasmodium wenyoni* Garnham, 1966 of Brazilian snakes as having such a maximum merozoite count rather than *Carinamoeba*, but it is ambiguous, for earlier (p. 818) 12-14 nuclei were stated to be produced by *P. wenyoni*. *Ophidiella* was proposed as a subgenus by Garnham to distinguish the poorly known *Plasmodium* parasites of snakes from those of saurians.

Twenty-three saurian *Plasmodium* species were recognized by Garnham when he erected the subgenera. Two others, *Plasmodium brumpti* Pelaez and Perez-Reyes, 1952 and *Plasmodium beltrani* Pelaez and Perez-Reyes, 1952 were omitted, while description of another Mexican species, *Plasmodium josephinae* Pelaez, 1967 had not appeared. Since 1966, 34 additional species and subspecies of haemosporidians here considered to be *Plasmodium* have been described from Neotropical lizards, two from North America, four more from Asia, one from Australia, and eleven from Africa. Descriptions of a dozen more are in preparation. The variety of species found in the last twenty years demands subgeneric reclassification into more precisely defined groups if possible, which reflect their common characteristics but which do not depart further than necessary from the basic scheme of classification provided by Garnham (1966) for mammalian and avian species. It was perhaps inevitable that the discovery of so many new species produced some which do not easily fit the clear-cut definitions of haemosporidian families and genera provided by Garnham, so readily accepted at that time.

The classical definition of the Plasmodiidae, as given by Garnham (1966) follows: " Plasmodiidae Mesnil, 1903. Parasites belonging to this family have a sexual phase in the mosquito and asexual cycles in tissue and blood cells of the vertebrate host; gametocytes are produced and are confined to mature erythrocytes. Malaria pigment is present in certain stages of the parasite." Garnham recognized a single genus within the Plasmodiidae; the definition of *Plasmodium*, therefore, is that of the family. The critical characters of this definition relate to the mosquito host, asexual cycles in both tissue and blood

cells, the production of gametocytes and their restriction to erythrocytes, and the presence of malaria pigment (hemozoin). Neither type of host cell nor production of a visible metabolic residue, in my opinion, represents a biologically or evolutionarily significant characters for definition of higher taxa. Both Ayala (1977) and Levine (1985) have expressed a similar viewpoint.

In 1969 and 1970 I described three saurian malarias from Panama which did not show visible pigment: *Plasmodium balli*, *Plasmodium gonatodi*, and *Plasmodium morulum*. Although *P. balli* was reported as having pigment, "minute black dots" or "mass larger than a single merozoite" (Telford, 1969) this was not confirmed as hemozoin under polarized light, and re-examination of the type slides on several occasions since has not confirmed its presence. I can only conclude that I was mistaken in describing the occasional presence of pigment in this species. In 1973 I reported the presence of pigment in some gametocytes of *P. morulum*. This was confirmed under polarized light, and it is difficult to consider this to be error. The sample in question was from an experimental infection in at least the fourth passage of the original isolation of *P. morulum*, which makes it most unlikely that another, pigmented species was also present but undetected that long. *Plasmodium azurophilum* from the Caribbean is typically unpigmented (Telford, 1975), but pigment was observed in 0.2 percent of the gametocytes (N= 800+), and confirmed under polarized light as hemozoin. In the other unpigmented species which I have studied--*Plasmodium scorzai* and *Plasmodium lainsoni* (Telford, 1978) and *P. gonatodi* (Telford, 1970)--I have never detected pigment. Although *Plasmodium beebei* (Telford, 1978) appears closely related to *P. gonatodi* by having very similar, bizarrely shaped "prematuration" gametocytes, it is pigmented. Another normally pigmented species, *Plasmodium tropiduri panamense*, is often seen without pigment in gametocytes and seldom shows pigment in schizonts. Here, the presence of pigment is correlated with maturity of host cell: those found in erythrocytes are more frequently pigmented than are those which occupy immature red blood cells (Telford, 1979). *Plasmodium telfordi*, was described as unpigmented by Lainson, Landau, and Shaw (1973). I found morphologically indistinguishable parasites in the same host, *Ameiva ameiva* from Guyana, which were frequently pigmented (Telford, 1973). Later, in Venezuela (1980), I found apparent *P. telfordi* infections in *A. ameiva* to be consistently pigmented--yet found a single infection that was almost entirely unpigmented. The host cells for this latter infection were mostly proerythrocytes.

From the above observations I have concluded that the production of visible pigment by some saurian malarial species is a variable character, correlated with parasitizing immature erythrocytes, and is therefore unreliable as a single criterion for subgeneric or generic classification. Other species, however, never (or very rarely) produce hemozoin, despite occupying erythrocytes, and these may form a natural group taxonomically. Lainson,

Landau and Shaw (1971) erected a separate family and genus, Garniidae and *Garnia* for four species which lacked pigment visible under light microscopy. Although I did not accept their taxa at the levels proposed (Telford, 1973), I commented that *Garnia* might be valid as a subgenus of *Plasmodium*, and it will be used thus in the classification presented below.

In 1970 I reported the presence of gametocytes and schizonts in thrombocytes and lymphocytes of Panamanian lizards which showed patent erythrocytic infections of *Plasmodium floridense*, *Plasmodium tropiduri*, and *Plasmodium aurulentum*. I suggested two possible interpretations (Telford, 1970): "(1) The exoerythrocytic forms represent one or (probably) more malaria-like species which parasitize white blood cells exclusively or (2) These stages are part of the mechanism whereby latent infections can again give rise to patent parasitemia of the erythrocytes." Scorza (1971) then reported thrombocytic gametocyte infections in Venezuelan lizards infected with *P. tropiduri*. Finding additional infections of malaria-like parasites in thrombocytes and lymphocytes of Brazilian lizards, Lainson, Landau, and Shaw (1974) erected a genus, *Fallisia*, within their family of unpigmented parasites, the Garniidae, distinguished by supposed absence of an erythrocytic cycle, schizogony and gametogony occurring solely within thrombocytes and leucocytes. This position coincided with my first interpretation, cited above. Their view, apparently, was that saurian malaria species known to parasitize one series of cells (erythrocytic) lack the capacity to utilize another lineage (leucocytic). However, pioneer studies by Thompson and Huff (1944) described the capacity of *Plasmodium mexicanum* to parasitize virtually all cell lineages in infections induced by inoculation of blood. In addition, Scorza (1971) provided substantial evidence that *P. tropiduri* possesses both erythrocytic and thrombocytic schizogonic and gametogonic cycles. Until recently, no evidence has been produced from experimental infections to preclude the possibility that thrombocytic/lymphocytic infections described as *Fallisia* were not preceded by erythrocytic cycles. The usually unpigmented *Plasmodium azurophilum* has both erythrocytic and leucocytic cycles of schizogony and gametogony, for which I suggested (Telford, 1975) that the non-erythrocytic cycles may represent a defense against immunity raised by a possibly brief but intense erythrocytic infection. If only leucocytic stages were available, as is commonly seen in natural infections, one might find it difficult to distinguish *P. azurophilum* from *Fallisia audaciosa* Lainson, Shaw and Landau, 1975. Experimental evidence is now available, derived from study of an avian parasite by Gabaldon, Ulloa, and Zerpa (1985), which demonstrates that the leucocytic cycle of *Fallisia neotropicalis* is not preceded by an erythrocytic cycle. Pending confirmation of these results for a saurian *Fallisia* species, I can accept *Fallisia* as a genus of the Plasmodiidae, comprised of those species for which only thrombocytic or leucocytic cycles are known.

An additional element of the classical definition of *Plasmodium* is the restriction of vector group to mosquitoes. When life cycles of reptilian plasmodiids were unknown, this was perhaps a useful criterion, being based upon data from avian and mammalian species only. However, Ayala (1971) demonstrated that *P. mexicanum* readily underwent sporogony in two species of phlebotomine sandflies, *Lutzomyia vexator* and *L. stewarti*, and more recently Petit et al. (1983) obtained the sporogony of *Plasmodium agamae* in a European ceratopogonid, *Culicoides nubeculosus*. Klein (1985) succeeded in transmitting *Plasmodium floridense* by *Culex erraticus* and confirmed Ayala's work by obtaining transmission of *P. mexicanum* by bite of infected *Lutzomyia vexator*. Ultrastructural studies of *P. floridense* by Aikawa and Jordan (1968), *P. mexicanum* by Moore and Sinden (1973), and *P. tropiduri* by Scorza (1971) have demonstrated that there is no significant difference between reptilian and avian malarial parasites in the morphology of erythrocytic stages, while the ultrastructure of the sporogonic forms of *P. floridense* by Klein (1985) and *P. agamae* by Boulard et al. (1983) again confirms their generic identity with *Plasmodium*. It is appropriate to point out the parallel capacity of adeleid haemogregarines and lankesterellid coccidia of reptilian hosts to utilize opportunistically a variety of haematophagous vectors for transmission. This suggests that reptilian haemosporozoa retain primitive characters which were of adaptive significance long before vertebrate divergence produced the reptilian lines which evolved into the birds and mammals of today.

The only components of the classical definition of *Plasmodium* that are applicable to all reptilian, avian and mammalian species are the presence of asexual and sexual cycles in blood cells and tissues of the vertebrate host and the production of gametocytes. Levine (1985) has re-defined both the family and the genus in terms broad enough to include all of the known reptilian haemosporidia: "Macrogamete and microgamont develop independently; conoid ordinarily absent; syzygy absent; microgamont produces 8 flagellated microgametes; zygote motile (ookinete); sporozoites naked, with 3-membraned wall; endodyogeny absent; heteroxenous, with merogony in vertebrate host and sporogony in invertebrate; pigment (hemozoin) visible with light microscope, may or may not be formed from host-cell hemoglobin; transmitted by blood-sucking insects." Although definite proof of an asexual cycle in circulating leucocytes has not been obtained yet for *Saurocytozoon*, there is circumstantial evidence that it exists. I found large intralymphocytic schizonts present during the first forty days of an initial *S. tupinambi* infection in a juvenile *Tupinambis teguixin*; the schizonts vanished from peripheral blood smears when mature gametocytes appeared (Telford, 1978). Later (Telford, 1983), I reported apparent schizonts in lymphocytes of *Mabuya multifasciata* infected with *S. mabuyi*. These observations must be confirmed from experimental infections induced by sporozoites. Certainly the sporogonic pattern of *S. tupinambi*, as described by Landau et al. (1973), justifies its classification as a plasmodiid

(Telford, 1983). When the two described species are better known, perhaps *Saurocytozoon* might be recognized as a subgenus of *Plasmodium*. At present, it is reasonable to consider it as a plasmodiid genus (Telford, 1983; Levine, 1985).

As mentioned above, it is desirable to provide subgeneric groupings of the known reptilian malarias, using criteria similar to those employed by Garnham (1966) for the definition of mammalian and avian subgenera. He relied upon two erythrocytic stages to separate the subgenera, gametocyte shape and schizont size. Sufficient information is known about many of these parasites to provide other more basic and useful characters for subgeneric definitions, but they can be grouped by erythrocytic schizonts and gametocytes alone. With the reptilian malarias we have virtually no useful characters other than those provided by the erythrocytic stages. I presented some tentative groupings in 1974, using the range of merozoite mean number and gametocyte size (length X width, LW), supported by less important characters such as pigment presence, gametocyte sexual dimorphism, and host cell types. These groups were based upon study of New World species only, although it was possible to assign most of the Old World forms to them. Ayala (1977) provided similar groupings to mine, using also the relationship of parasite size to host cell nucleus size. Neither of these attempts to group related species was based upon adequate morphometric comparisons.

In the past decade I have obtained considerably more material, especially from Africa, but including several species from Southeast Asia as well. The classification proposed below is based primarily upon morphometric comparisons, derived from measurements of 17,906 parasites--7213 schizonts and 10,693 gametocytes, obtained from 316 infections comprised of 115 host-parasite combinations. There are 67 species and subspecies of *Plasmodium* represented, distributed as follows: 6 North American, 19 Middle American, 18 South American, 5 Caribbean, 1 Australian, 4 East-Southeast Asian, and 21 African-Madagascan. Some species (Middle and South American) were studied from more than one area. Data are included from five species and subspecies (Africa, Hispaniola, Panama, and the Philippines) presently under description. These 67 species and subspecies represent 79 percent of those 85 forms known by me to exist.

ACKNOWLEDGEMENTS

Many people have assisted in this work over the last 20 years, most with no expectation of significant results, for progress has been slow. The preparation and screening of blood smears from over 15,000 lizards, the study of infections found, the measurement of series of parasites, their frequent taxonomic description accompanied by the taking of photomicrographs and drawings, seemingly endless analysis of data, and evaluation of combinations of characters have

all consumed my time and energy. Very little of this work could be done during the normal working day, for I have never been fortunate enough to be employed as a student of either malarial parasites or their saurian hosts. My professional obligations to the Gorgas Memorial Laboratory, the University of Florida, the World Health Organization, and the Danish International Development Agency have held first priority, although when time permitted it certainly must have appeared to my superiors that my interest in saurian malaria came first! Hopefully my productivity on the various projects for which I was engaged by those agencies reduced to some degree the anxiety of my superiors. Only the most efficient use of personal time made it possible to produce the body of work which resulted in this contribution.

I wish to thank the following individuals for their help in the acquisition of the lizard hosts or blood slides: the late Howard W. ("Duke") Campbell, Richard C. Goris, Walter Auffenberg, Richard Franz, Steven P. Christman, Peter Meylan, John B. Iverson, C. A. Smith, Paul Moler, Sylvia Scudder, David G. Young, Stephen C. Ayala, J. V. Scorza, John E. Lovett, William R. Smythe, Kim Howell, John Hall, Richard D. Sage, G. Gorman, A. Lowichik, T. A. Burns, and C. H. Lowe. A very distinguished group of senior scientists through the years have provided the very best professional knowledge or contributed blood slides, furnished administrative support, and served as role models through their interest, friendship, and above all else, constructive criticism, and to them I am deeply indebted: P. C. C Garnham, Martin D. Young, Manabu Sasa, the late Gordon H. Ball, the late L. A. Stauber, and the late C. G. Huff. I wish to thank Jerry F. Butler for his administrative support toward publication of this study, during a most difficult transition period for me. I have had the pride and joy of watching three small boys grow into manhood enthusiastically catching every lizard sighted as we explored together the rice fields of Japan, the deserts and mountains of the American southwest and Pakistan, the tropical forests of Panama and Venezuela, the urban parks of Southeast Asia, the East African savanna and montane rainforest, and the woods, swamps and neighborhoods of North Florida. Sam, Randolph, and Robert collected the hosts of probably one-third of the malaria species I subsequently described as new, and their assistance is missed as their own careers develop. My wife, Michiko, has helped me in countless ways during three decades, providing the domestic stability without which this work could not have been done.

MATERIALS AND METHODS

I have elsewhere (Telford, 1974, 1979) described 21 characters of possible taxonomic utility in defining saurian *Plasmodium* species. Most of them await proper statistical evaluation, because the very large number of parasites examined precludes their use until all data have been properly prepared for multivariate analysis by computer. I chose five characters to consider for definition of subgenera: size of gametocyte and schizont (maximum length X maximum width, or LW), merozoite number, gametocyte shape (length/width, or L/W), and gametocyte-schizont size relative to erythrocyte nucleus size. I have discarded gametocyte shape in the present analysis. Although useful in the definition of many species, where 95 percent of gametocytes may show a characteristic form (elongate, oval or round, bulky), in other species there is a clear correlation between gametocyte shape and the position of the gametocyte within the host cell. In the most euryxenous saurian *Plasmodium*, for instance *P. floridense*, gametocyte shape is significantly correlated (by chi square test) with position: those gametocytes with an L/W ratio of 1.7+ tend to occupy lateral or lateropolar positions, while those with round (1.0-1.39) or oval (1.4-1.69) configurations occupy polar positions. The comparison was run on 1318 gametocytes from infections of 11 *Anolis* and 2 *Sceloporus* species. Schizont size is correlated with merozoite numbers in some species but not in others, but I have decided to use this characteristic in subgeneric definitions because it is easily compared with erythrocyte nucleus size. As with gametocyte shape, the configuration of saurian *Plasmodium* schizonts is too variable in most species to permit simple generalizations to describe shape, and thus was not used here for subgeneric definitions.

A simple comparison of gametocyte or schizont size with the nucleus of the parasitized cell introduces other variables into this relationship: the effect the parasite has upon the host cell nucleus. Many species do cause hypertrophy, hypotrophy, or mild to severe distortion and even lysis of the host cell nucleus. While nuclei of mature erythrocytes vary within comparable limits to that seen for gametocytes and schizonts, nuclei of erythroblasts and proerythrocytes are far more variable, both in shape and size. Immature cells are often parasitized by asexual stages in particular, and in some cases, preferentially. It was desirable, therefore, to provide an objective standard against which size comparisons could be made, one always available and subject to the same techniques of fixation, staining and measurements as the parasites themselves, yet independent from possible effects of parasitism. The size (LW) of nuclei from uninfected, mature erythrocytes provides this standard. By using samples of nuclei from the slides examined, the significant differences that exist in erythrocyte nucleus size among host families, genera and species groups can be disregarded. Accordingly, I have plotted ratios of mean schizont size to mean erythrocyte nucleus size against ratios of mean gametocyte size to the same nucleus mean size for each infection studied. Both ratios have been plotted against the range of merozoite numbers observed in the same infection. Mean merozoite number is too susceptible to the influence of infection phase, commonly being lower following the infection peak of parasitemia. The range of merozoite numbers is much more similar during each phase of infection (early, pre-peak, post-peak, chronic, and recrudescent or relapse phases) than is the mean in most of the species I have studied. The point chosen for plotting against the schizont and gametocyte size ratios is the midpoint of the observed range. The location of a sample within the triangle formed by these three characters provides a locus which can be considered to be the phenotype of the given species as defined by these characters. Incorporation of additional characters would, of course, change the locus but, hopefully, not the groupings of the species.

Additional considerations have influenced the graphical presentation of the data. For simplicity in presentation, all means used and the range midpoint of merozoites have been converted to log values. Of the 67 species and subspecies studied, one (*Plasmodium maculilabre*) was represented only by gametocytes, no mature schizonts being present on the slides examined. These could not be plotted. The plotting of individual infections measured—over 300—found many points representing the individual infections overlapping, both within species of which several infections were measured and among species. However, if an average of the mean values or merozoite range midpoints is used, most of the overlap disappears, and species can be represented upon the graph by a single number, that associated with the host-parasite association listed under Material Examined. Morphometric data have not been used to define two subgenera recognized here, *Garnia* and *Ophidiella*, and they are therefore not included in the figures.

All measurements were taken by me with the same microscope (a Nikon STR) and the same ocular micrometer, calibrated at 1000X, under oil immersion. The usual samples taken were 25 gametocytes, 25 mature or segmenting schizonts, and 10 uninfected erythrocytes. With undescribed species, species where few infections could be obtained, or when infections were intense, thus reducing the time involved to locate parasites, sample size was often increased to 50 or more of each stage. When possible, three infections from each host-parasite association were studied, and in some cases more. Some, however, are represented by only a single infection (36%), and not all samples of each stage were adequate for plotting. Selection of parasites for measurement was as unbiased as possible: the first seen which showed the following criteria were measured, and each subsequent parasite until the desired sample had been found. Gametocytes were chosen on the basis of apparent maturity: sexual differentiation by staining reaction, and dispersal of pigment from the clumped mass seen in immature gametocytes of virtually all species studied. Those few species that show focused pigment when apparently mature were chosen by comparison of staining reaction and size to obviously immature gametocytes. Schizonts selected for measurement were either segmenting or those in which nuclear division had evidently been completed, but discrete merozoites were not visible. Use of this latter category cannot be defended except by pleading experience of the investigator. For gametocytes and schizonts, maximum length and maximum width were measured, which provided the character length X width (LW). Schizonts were selected for measurements only if the number of merozoites or nuclei could be counted. Uninfected erythrocytes from each infection studied were those which showed no distortion from the act of smearing the blood on the slide, or from lysis. Maximum

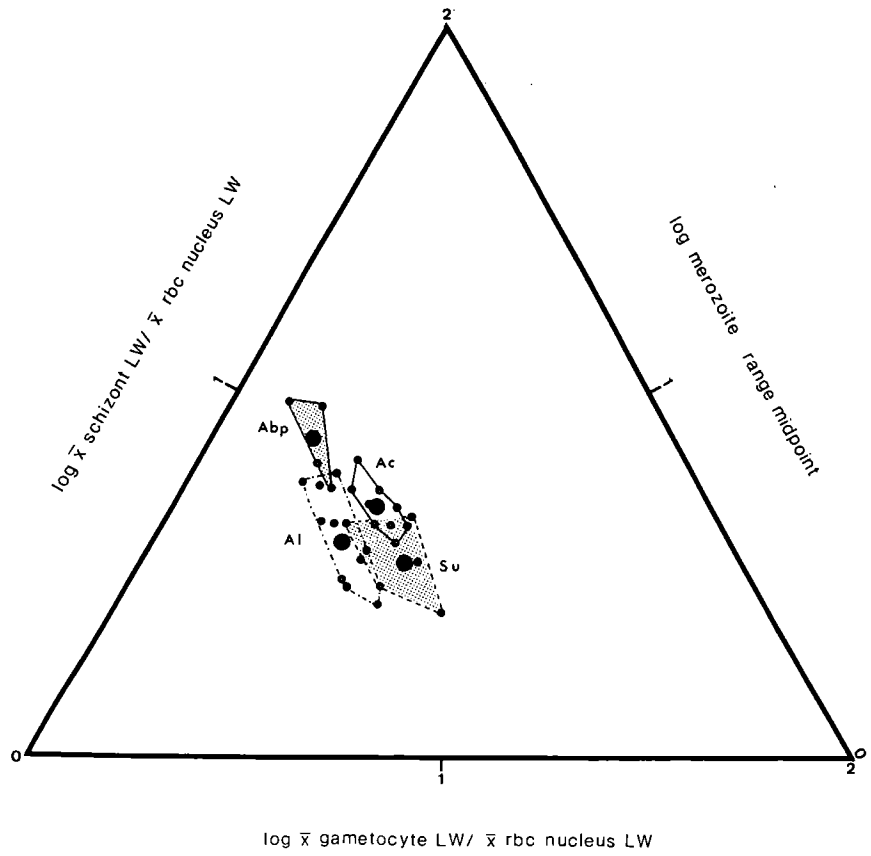

Figure 1. Distribution of individual *Plasmodium floridense* samples from four host species around mean values for each host-parasite association. Abbreviations represent *Sceloporus undulatus* (Su), *Anolis carolinensis* (Ac), *Anolis limifrons* (Al), and *Anolis biporcatus* (Abp).

length and width was recorded for both the cell and its nucleus. Cell dimensions were also routinely recorded for those mature erythrocytic cells containing measured parasites, as were the other characters described earlier (Telford, 1974, 1979). All slides examined had been fixed in absolute methanol and stained by Giemsa or May-Grunwald Giemsa techniques.

RESULTS

In Figure 1 multiple samples from four saurian species host to *Plasmodium floridense* have been plotted around the mean of all samples from the

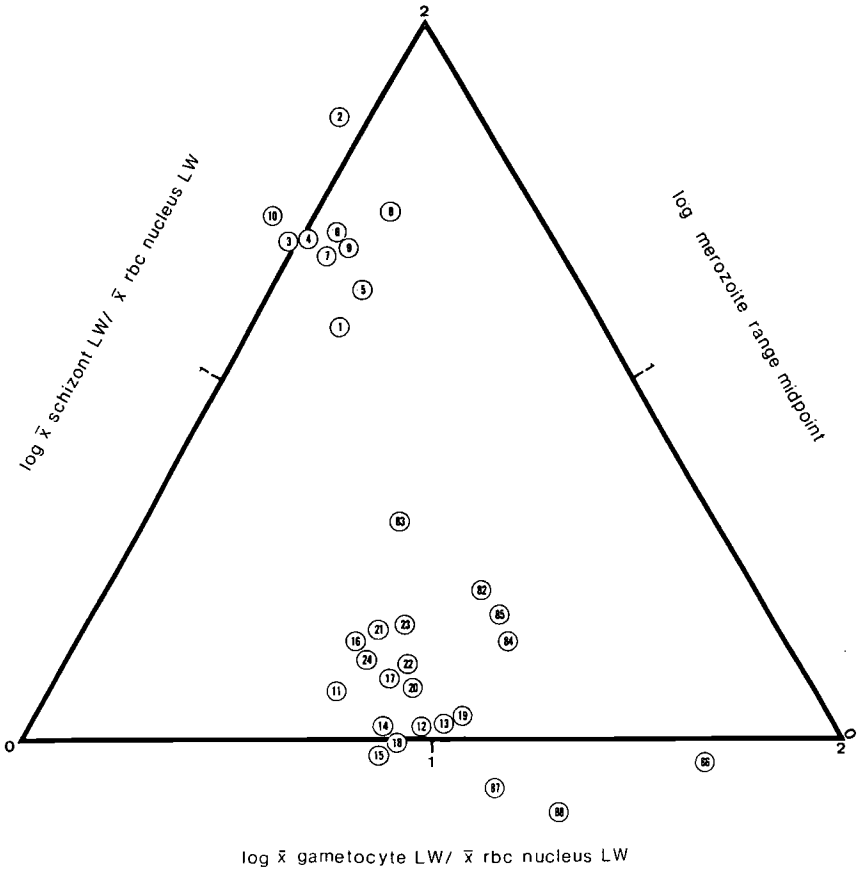

Figure 2. Separation of saurian *Plasmodium* species (from both Eastern and Western Hemispheres) by means of morphometric characters plotted against midpoint of the observed merozoite range. Sample numbers refer to each host-parasite association listed under Material Examined. Samples 1-10 are species with large gametocytes and schizonts; 11-24 have small gametocytes and schizonts; 82-85 have large gametocytes and medium sized schizonts; 86-88 have schizonts disproportionately smaller than gametocytes.

particular hosts. The observed variation found in the samples from a given host-parasite association lies within certain limits around the point representing the overall average. It is probable that this variation can be attributed largely to infection phase which can influence gametocyte or schizont size, or merozoite range. Figure 2 demonstrates the presence of two groups of *Plasmodium* species widely separated by size of both gametocytes and schizonts: very large and very small. The group of larger species contains within it *Plasmodium diploglossi* Aragao & Neiva, 1909, type species of the

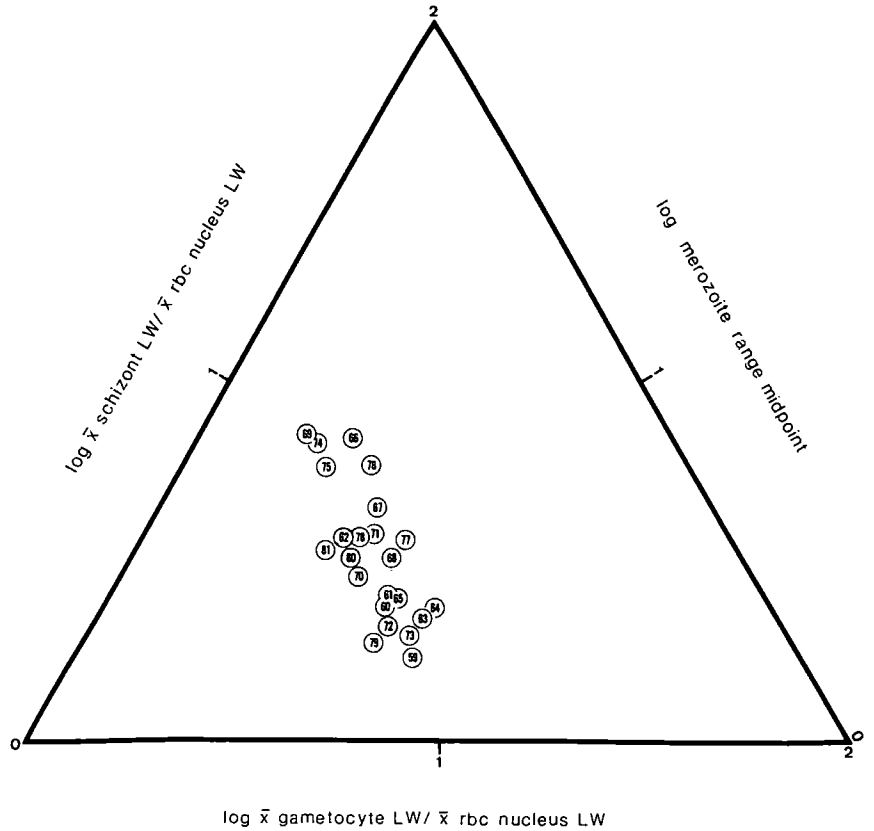

Figure 3. Samples from Neotropical *Plasmodium* species that have gametocytes and schizonts of similar size, intermediate between *Sauramoeba* and *Carinamoeba* species.

subgenus *Sauramoeba* Garnham, 1966. The smallest species include *Plasmodium minasense* Carini & Rudolph, 1912, type species of *Carinamoeba* Garnham, 1966. I recognize these subgenera as valid groups of morphometrically related species.

There exists, however, a very large number of species that lie in between *Sauramoeba* and *Carinamoeba* in their morphometric characters (Figs. 3-6). They are cleanly separated from *Sauramoeba* (Fig. 7). Some species, however, do overlap with *Carinamoeba* through the influence, usually, of having smaller schizonts which contain, however, more merozoites than typically seen in *Carinamoeba* species (Fig. 7). The midpoint in range of merozoite number for *Carinamoeba* is less than 8, i.e. 4-10 merozoites are produced by three normal

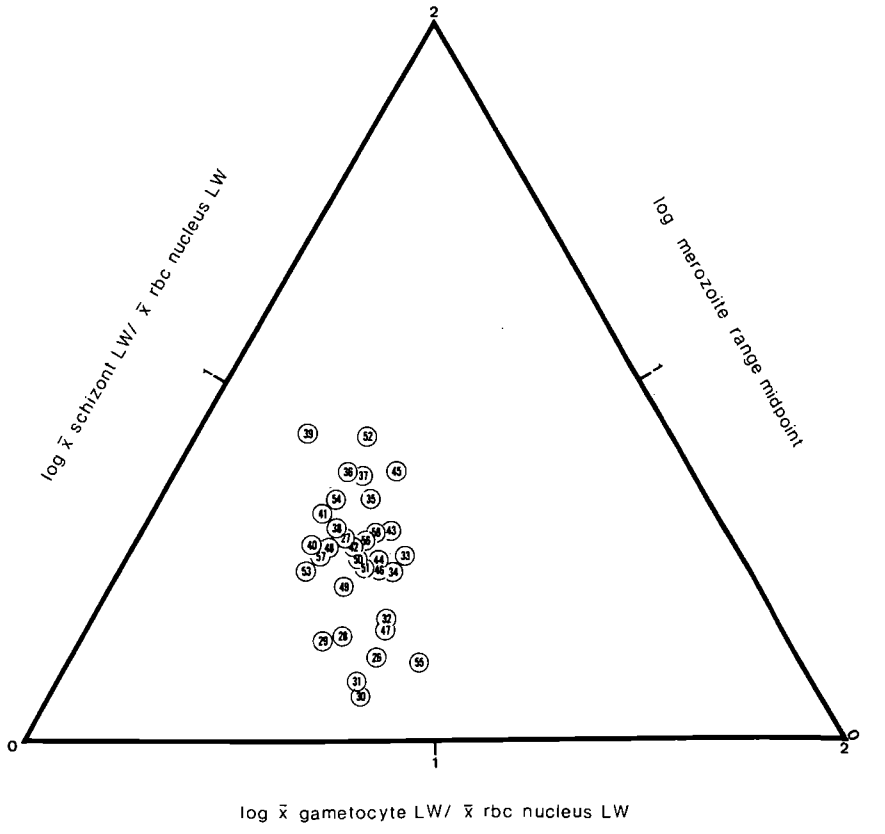

Figure 4. Samples from Old World *Plasmodium* species that have gametocytes and schizonts of similar size, intermediate between *Sauramoeba* and *Carinamoeba* species.

nuclear divisions, with occasional nuclei undergoing an extra division; this produces a greater effect upon midpoint of range than upon mean. The intermediate sized species undergo four or five nuclear divisions, with a range midpoint of 8 or more, i.e. 4-12+. *Plasmodium basilisci* Pelaez & Perez-Reyes, 1959 is a case in point. In the type host, *Basiliscus vittatus*, it produces 4-8 merozoites, which would place it in *Carinamoeba*. Infections in *Basiliscus basiliscus* usually show the same range in numbers but when immature erythrocytes are parasitized, up to 14 merozoites can be found (Telford, 1972). Its relationships morphometrically, then exclude it from *Carinamoeba*.

If the intermediate sized species from both Western (Fig. 3) and Eastern (Fig. 4) Hemispheres are plotted together (Figs. 5, 6), the combined polygon, formed by means of the various host-parasite associations, contains within it

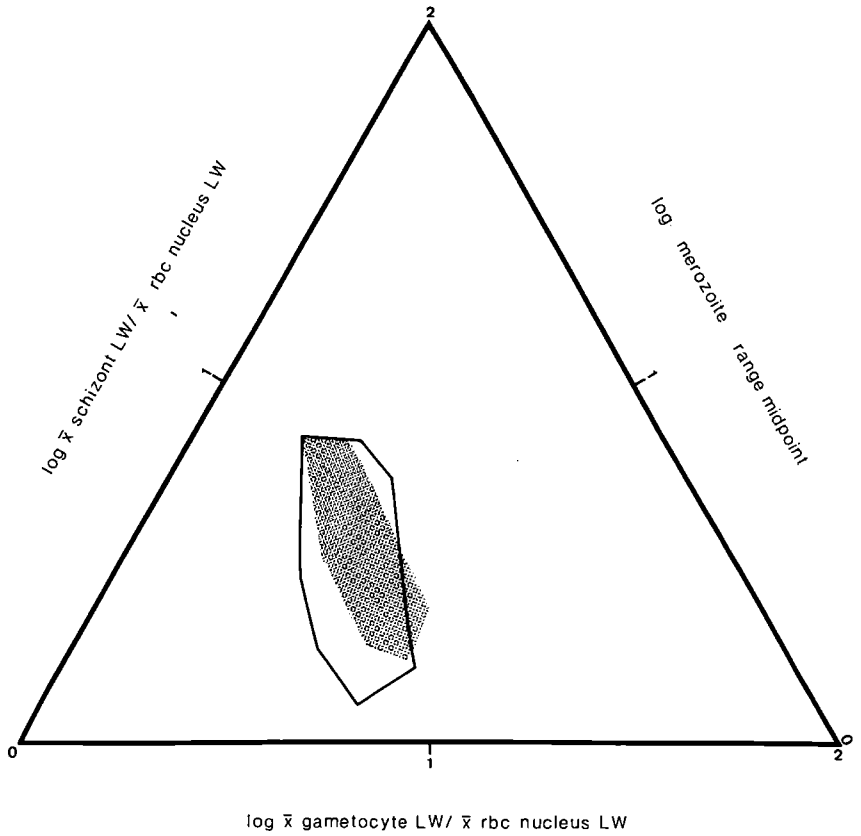

Figure 5. Combined polygons formed by samples depicted in Figures 3 (Neotropical) and 4 (Old World), representing the subgenus *Lacertamoeba*.

104 (76 %) of the 137 individual samples (Fig. 6). Enough material from both Africa and the Western Hemisphere has been examined to demonstrate that the same three basic groupings of large, intermediate, and small species occur in both areas (Figs. 2, 5). I believe that this justifies recognition of a third subgenus of pigmented *Plasmodium* species from lizards, intermediate in size between *Sauramoeba* and *Carinamoeba*. It is described below as subgenus *Lacertamoeba*.

Four additional subgenera can be recognized at present. One of these is *Garnia* Lainson, Landau and Shaw, 1971, to which I assign all unpigmented erythrocytic species in which the absence of pigment is not related to parasitization of immature erythrocytic cells. If *Garnia* were to be plotted in Figure 7 with the pigmented subgenera, one species, *Plasmodium balli*, would

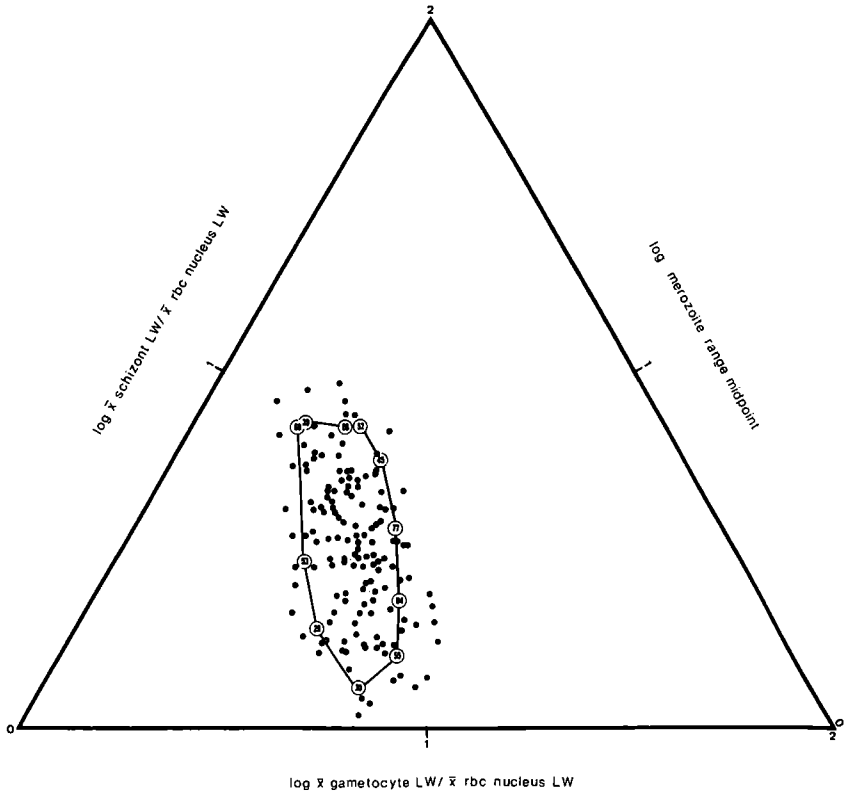

Figure 6. Distribution of individual Neotropical and Old World samples (solid circles) in relation to the polygon representing the subgenus *Lacertamoeba*. Numbered circles represent species that form the polygon boundary within which all other species means are included.

clearly lie within *Sauramoeba* and the remaining eight species within *Lacertamoeba*, which suggests that pigment presence or absence may be a derived rather than basic character. Until the significance of pigment presence or absence and its variability within individual infections is better understood, the definition provided here for *Garnia* must suffice. Although I have recently considered *Fallisia* to be a subgenus of *Plasmodium* (Telford, 1986), in Levine's classification (1985) *Fallisia* was synonymized with *Plasmodium*. The several species, though, evidently lack an erythrocytic cycle, with both schizogony and gametogony taking place in thrombocytes and leucocytes. It is possible that another explanation may yet be found for this choice of host cell, but on present knowledge, in view of the findings of Gabaldon et al. (1985), it

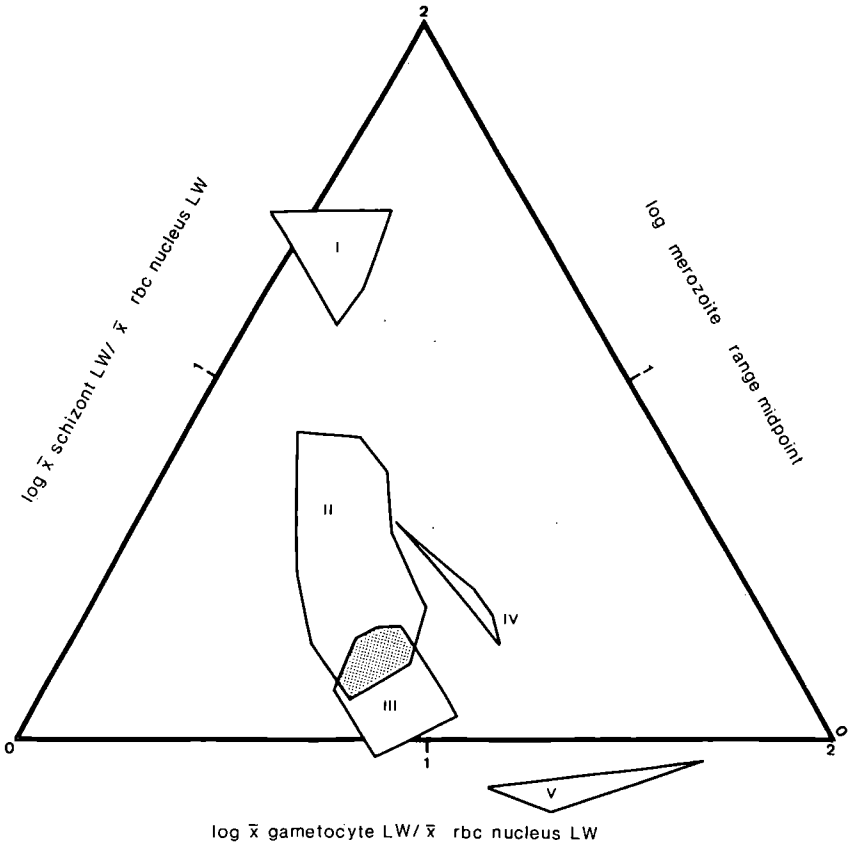

Figure 7. Morphometric relationships of the pigmented saurian *Plasmodium* species: I, subgenus *Sauramoeba*; II, subgenus *Lacertamoeba*: III, subgenus *Carinamoeba*; IV, subgenus *Paraplasmodium*; V, subgenus *Asiamoeba*. Shaded area represents overlap of *Lacertamoeba* with *Carinamoeba* species, schizonts of which undergo 3 nuclear divisions in comparison to 4 or 5, normally, for *Lacertamoeba*.

is reasonable to recognize *Fallisia* as a genus of the Plasmodiidae, as stated above. Garnham (1966) erected *Ophidiella* as a subgenus to accommodate *Plasmodium* species of snakes. *Ophidiella* is too poorly known for critical definition: there are three described species, one of which (*Plasmodium tomodoni*) could represent an ophidian member of *Sauramoeba*, and two of which (*Plasmodium wenyoni* and *Plasmodium pessoai*) might be *Lacertamoeba* species. Until more data are available, therefore, I will follow Garnham (1966) in recognizing the subgenus as described, despite my reservations on the significance of host type in systematics. Two North American species, *Plasmodium mexicanum* and *P. chiricahuae*, do not fit well morphometrically

with *Lacertamoeba* species (Fig. 7). Their gametocytes are among the largest known, yet schizonts are of medium size. In *P. mexicanum* it is possible to produce exoerythrocytic schizonts in a variety of fixed and circulating cells by inoculation of infected blood into a clean host (Thompson and Huff, 1944a). Pathology can result from apparent occlusion of cerebral capillaries by these exoerythrocytic schizonts. This has never been reported for the *Lacertamoeba* species which have been studied in experimental infections: *P. tropiduri* (Scorza, 1970), *P. floridense* (Thompson and Huff, 1944b; Goodwin and Stapleton, 1955), and *P. sasai* (Telford, 1972). In addition, sporogony takes place in psychodid flies (Ayala, 1971; Klein, 1985), and these probably are the natural vectors (Ayala, 1973). Therefore, it is appropriate to place these two North American species into a separate subgenus which I designate *Paraplasmodium*. The poorly known Venezuelan species, *Plasmodium pifanoi* Scorza & Dagert, 1956 has very large gametocytes and medium sized schizonts, and on these grounds only can be included in this subgenus. Finally, there appears to be an Asian-Pacific group of pigmented species, still poorly known, which has the unlikely combination of disproportionately large gametocytes and tiny schizonts. *Plasmodium saurocaudatum* Telford, 1983, *P. lygosomae* Laird,1951, *P. vastator* Laird,1960, and *Plasmodium clelandi* Manawadu, 1972 can be placed in this subgenus, *Asiamoeba*.

Definition of Subgenera

Sauramoeba Garnham, 1966

Saurian *Plasmodium* species characterized by large schizonts and gametocytes. Mean schizont size is three to seven times that of uninfected erythrocyte nuclei. Schizonts undergo 4 to 7 nuclear divisions, producing 14-130 merozoites. Mean gametocyte size is two to five times that of nuclei from uninfected erythrocytes. Gametocytes are usually smaller than or equal to schizonts in size. Sexual dimorphism is usually present in gametocyte size: macrogametocytes are larger than microgametocytes. Gametogony occurs in the erythrocytic series. Pigment is always present. Secondary erythrocytic schizogony occurs in leucocytes. Sporogony is unknown.

Contained species: *diploglossi* Aragao & Neiva, 1909 (type); *cnemidophori* Carini, 1941; *achiotense* Telford, 1972; *beltrani* Pelaez & Perez-Reyes, 1952; *giganteum* Theiler, 1930; *robinsoni* Brygoo, 1962; *heischi* Garnham & Telford, 1984; *australis* Garnham, 1966; *egerniae* Mackerras, 1961; *guyannense* Telford, 1979.

Carinamoeba Garnham, 1966

Saurian *Plasmodium* species characterized by small schizonts and gametocytes. Schizont size averages smaller than that of uninfected erythrocyte nuclei. Schizonts undergo 2 or 3 nuclear divisions, typically producing 4-8 merozoites, rarely up to 12. Average gametocyte size may slightly exceed that of uninfected erythrocyte nuclei, but is usually somewhat less. Gametocyte size may be twice that of schizonts. Sexual dimorphism in gametocyte size may occur but is not characteristic of most species. Pigment is always present in larger asexual stages and gametocytes. Gametogony occurs only in the erythrocytic series, usually in mature cells. Secondary exoerythrocytic schizonts may parasitize thrombocytes. Sporogony is unknown.

Contained species: *minasense* Carini & Rudolph, 1912 (type); *scelopori* Telford, 1977; *marginatum* Telford, 1979; *rhadinurum* Thompson & Huff, 1944; *attenuatum* Telford, 1973; *mabuiae* Wenyon, 1909; *cordyli* Telford, 1987.

Lacertamoeba **subgen. nov.**

Saurian *Plasmodium* species characterized by medium sized schizonts and gametocytes. Mean schizont size is one-half to twice that of nuclei from uninfected erythrocytes. Schizonts typically undergo 3 to 5 nuclear divisions; 4-55 merozoites may be produced. Average gametocyte size varies from slightly less than that of uninfected erythrocyte nuclei to twice their size. Gametocytes may be two and one-half times larger than schizonts, but more commonly slightly exceed schizonts in size. Pigment is usually visible; its absence is correlated with immaturity of host cells. Gametogony occurs in erythrocytes, but in some species thrombocytes or lymphocytes may host sexual stages. There is no consistent sexual difference in size of gametocytes. Where known, exoerythrocytic schizogony occurs in the reticulo-endothelial system, notably in the lymphoid macrophage series. Sporogony can occur in culicid and ceratopogonid flies.

Contained species: *tropiduri* Aragao & Neiva, 1909 (type); *floridense* Thompson & Huff, 1944; *brumpti* Pelaez & Perez-Reyes, 1952; *basilisci* Pelaez & Perez-Reyes, 1959; *josephinae* Pelaez, 1967; *aurulentum* Telford, 1971; *beebei* Telford, 1978; *torrealbai* Scorza & Dagert, 1957; *uncinatum* Telford, 1973; *vautieri* Pessoa & Biasi, 1973; *vacuolatum* Lainson, Shaw & Landau, 1975; *telfordi* Lainson, Landau & Shaw, 1971; *colombiense* Ayala & Spain,

1976; *iguanae* Telford, 1980; *sasai* Telford & Ball, 1969; *mackerrasae* Telford, 1979; *lacertiliae* Thompson & Hart, 1946; *agamae* Wenyon, 1909; *acuminatum* Pringle, 1960; *fischeri* Ball & Pringle, 1965; *maculilabre* Schwetz, 1932; *pitmani* Hoare, 1932; *zonuriae* Pienaar, 1962; *ulugurueńse* Telford, 1984; *loveridgei* Telford, 1984; *cnemaspi* Telford, 1984; *holaspi* Telford, 1986; *brygooi* Telford & Landau, 1987; *michikoa* Telford, 1988; *gogoloense* Telford, 1988; *tanzaniae* Telford, 1988; *uzungwiense* Telford, 1988; *arachniformis* Telford, 1988.

Paraplasmodium subgen. nov.

Saurian *Plasmodium* species characterized by medium sized schizonts and large gametocytes. Mean schizont size is one-half to twice that of uninfected erythrocyte nuclei. Schizonts undergo 3 to 5 nuclear divisions, producing 4-30 merozoites. Mean gametoctye size is three to six times that of nuclei from uninfected erythrocytes. Gametocytes are three to six times the size of schizonts. Pigment is always present in erythrocytic parasites. Gametogony occurs in erythrocytes. Sexual dimorphism is present in gametocyte size: macrogametocytes are larger than microgametocytes. Secondary exoerythrocytic schizonts may occur in fixed cells of the viscera and in circulating white blood cells. Sporogony can occur in psychodid flies.

Contained species: *mexicanum* Thompson & Huff, 1944 (type); *chiricahuae* Telford, 1970; *pifanoi* (?) Scorza & Dagert, 1956.

Asiamoeba subgen. nov.

Saurian *Plasmodium* species characterized by schizonts and gametocytes greatly disproportionate in size. Schizont size does not exceed one-fourth that of nuclei from uninfected cells. Schizonts undergo 2 nuclear divisions, producing 3-4 nuclei. Mean gametocyte size is four to eight times that of uninfected erythrocyte nuclei. Gametocytes are four to fifteen times larger than schizonts. Pigment is always present. Gametogony occurs in erythrocytes. Sexual dimorphism may be present in gametocyte size, with macrogametocytes larger than microgametocytes. Exoerythrocytic schizogony and sporogony are unknown.

Contained species: *saurocaudatum* Telford, 1983 (type); *lygosomae* Laird, 1951; *clelandi* Manawadu, 1972; *lionatum* Telford, 1982; *vastator* Laird, 1960.

Garnia Lainson, Landau & Shaw, 1971

Saurian *Plasmodium* species characterized by erythrocytic schizonts and gametocytes equal to or larger than uninfected erythrocyte nuclei, in which the absence of pigment is independent of host cell maturity. Pigment is rarely demonstrable. Schizonts undergo 3 to 7 nuclear divisions, producing 8 to 100 merozoites. Gametogony may occur in erythrocytes or in leucocytes during part of the life cycle. Gametocytes may show sexual dimorphism in size, with macrogametocytes usually larger than microgametocytes. Exoerythrocytic schizonts occur in thrombocytes and leucocytes. Sporogony is unknown.

Contained species: *gonatodi* Telford, 1970 (type); *morulum* Telford, 1970; *utingensis* Lainson, Landau & Shaw, 1971; *multiformis* Lainson, Shaw & Landau, 1975; *uranoscodoni* Lainson, Shaw & Landau, 1975; *scorzai* Telford, 1978; *lainsoni* Telford, 1978; *balli* Telford, 1969; *azurophilum* Telford, 1975.

Ophidiella Garnham, 1966

Ophidian *Plasmodium* species characterized by erythrocytic schizonts and gametocytes equal to or larger than uninfected erythrocyte nuclei. Schizonts undergo 3 to 6 nuclear divisions, producing 12 to 66 merozoites. Pigment is always present. Gametocytes may show sexual dimorphism in size, with macrogametocytes larger than microgametocytes. Exoerythrocytic schizogony and sporogony are unknown.

Contained species: *wenyoni* Garnham, 1966 (type); *tomodoni* Pessoa & Fleury, 1968; *pessoai* Ayala, Moreno & Bolaños, 1978.

DISCUSSION

The subgeneric classification presented above for the reptilian haemosporidia which I consider to be *Plasmodium* is open to criticism from at least three aspects. Those workers who insist that *Plasmodium* should include only those organisms which share all characters shown by the four species that parasitize humans--specifically the presence of pigment, restriction to erythrocytes in the vertebrate, and use of the Culicidae as vectors--will be

reluctant to accept the scheme. In a zoological, as opposed to historical, sense there is nothing special about the fact that the genus *Plasmodium* Marchiafava and Celli, 1885 was described from a species, *P. malariae*, which infects humans. Instead, I take the position that classifications, like species, are not immutable, and while I readily recognize new species on the basis of morphometric and qualitative traits, I prefer to conceive of the higher taxa of genus and family as showing probable evolutionary relationships. It is most unusual to demonstrate a derivative/phylogenetic relationship of one species group to another currently existing, except in a speculative manner based upon the experience of the systematist involved. Happily, with the advent of biochemical techniques that demonstrate actual sharing of portions of genomes, it should become possible to establish relationships in more objective terms than was previously possible for organisms which lack a fossil record.

Another anticipated criticism is my use of morphometrics as the basis for the classification. I can only respond that there is little else available yet for parasites of lower vertebrates besides those characters which can be gleaned from blood smears. Professor Garnham (1966) provided adequate justification for this approach to taxonomic characters: "The organisms are so small that what would constitute familial or even ordinal differences of the same proportions in larger animals, could easily pass unrecognized in the Protozoa; any character therefore should be seized and used as liberally as possible."

The third possible objection will be that there are too many subgenera of reptilian plasmodiids in comparison to mammals and birds. Garnham (1966) proposed three subgenera for mammalian parasites: *Plasmodium*, *Laverania*, and *Vinckeia*. Avian *Plasmodium* species were placed in four: *Haemamoeba*, *Huffia*, *Novyella*, and *Giovannolaia*. Here, I suggest that there are seven groups of possibly related species found in reptilian hosts: *Sauramoeba*, *Carinamoeba*, *Lacertamoeba*, *Paraplasmodium*, *Asiamoeba*, *Garnia*, and *Ophidiella*. *Fallisia* and *Saurocytozoon* deserve generic status, which is a different problem. Given the fact that there are now as many described and known but yet undescribed species and subspecies of reptilian plasmodiids as there are avian and mammalian species together, I do not think there is an excessive number of subgenera. Plasmodiids have been reptilian parasites far longer than they have utilized mammalian and avian hosts, and increased diversity of both species and species groups is to be expected.

The topics of variation and ecological zoogeography will not be discussed here in detail, as I intend to address them in future papers. It is obvious, though, from the information presented here, that not all of the reptilian genera and subgenera are cosmopolitan in their distribution. To a considerable degree this represents the geographical distribution and intensity of investigative effort, which has been greatest in the Western Hemisphere and East Africa. The distribution of subgenera and genera can be briefly summarized as follows: *Sauramoeba* is known from Mexico to Brazil,

throughout Africa and on Madagascar, and from Australia, but not yet from Asia; *Carinamoeba* occurs from Mexico through Brazil, in the Caribbean, Africa, and Southeast Asia; *Lacertamoeba* is found throughout the Western Hemisphere, Africa, Madagascar, Southeast and East Asia, and Australia; *Garnia*, *Ophidiella*, and *Paraplasmodium* are known only from the Western Hemisphere; *Asiamoeba* is found in Southeast Asia and New Zealand; *Fallisia* occurs in the Neotropics from Brazil at least into Panama, in the Caribbean, and in Southeast Asia and the Australasian region; *Saurocytozoon* is found in northern South America and in Southeast Asia. Three important areas are yet poorly known--Southeast Asia, Australasia, and the West and Central African rainforest. Sustained field efforts in these areas should clarify the distribution of reptilian haemosporidia and hopefully shed additional light upon their relationships. The classification provided here should be tested by studies on sporogony and exoerythrocytic schizogony and by biochemical procedures to determine the relevance of morphometrics to systematics of the Haemosporidia.

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MATERIAL EXAMINED

The material listed below was examined during the period 1967-86. Except where noted, all slides are in the Telford collection or have been deposited as paratype material as indicated in earlier taxonomic papers. Voucher specimens of hosts for all material I have collected is deposited at the Florida State Museum, Gainesville. Unless another source is indicated, I have personally obtained the hosts and prepared the slides. Numbers preceding the taxonomic name identify the species or samples in the figures. The letters S and G refer to the stages measured, schizont and gametocyte, respectively, while N and E indicate type of infection, natural or experimental. Host species immediately follows the *Plasmodium* specific name. TYPE indicates that I have examined the type slide.

SAURAMOEBA

1. *diploglossi*: *Mabuya mabouya*, 110 S, 125 G, 2 N & 2 E ex Panama, San Blas Terr., 5 km W Mulatupo, Sasardi.

2. *cnemidophori*: *Ameiva ameiva*, 85 S, 125 G, ex Panama, Canal Zone, Madden Dam, 1 N; Guyana, Georgetown vic., 1 N; Venezuela, Est. Portuguesa, Mun. Nueva Florida, Santo Domingo, 1 N; Estado Guarico, Mun. Ortiz, Los Cumbitos, 1 N.

3. *guyannense*: *Plica plica*, 23 S, 29 G, ex Guyana, Georgetown vic., 1 N, TYPE.

4. *achiotense*: *Basiliscus basiliscus*, 25 S, 75 G ex Panama, Colon Prov., Achiote village, 1 N, TYPE; Panama Prov., El Aguacate, 1 N.

5. *beltrani*: *Sceloporus teapensis*, 50 G, ex Mexico, Est. Veracruz, Region de los Tuxtlas, 1 N (D. Pelaez).

   beltrani: *Sceloporus malachiticus*, 15 S, 50 G ex Mexico, Est. Chiapas, 3.9 km N Rincon Chamula, 1 N.

6. *giganteum*: *Agama agama*, 50 S, 50 G ex Zaire, 12 km WSW Kinshasa, Kinsuka on Congo R., 2 N.

7. *giganteum*: *Agama mossambica*, 50 S, 75 G ex Tanzania, Morogoro Region, Morogoro, N Slope Uluguru Mtns at Univ. Campus, 2 N.

8. *heischi*: *Mabuya striata*, 25 S, 100 G ex Kenya, Nairobi, 2 N, TYPE (London, P.C.C. Garnham).

9. sp. indet.: *Mabuya striata*, 25 S, 50 G ex Kenya, Nairobi, 1 N.(London, P.C.C.Garnham).

10. *robinsoni*: *Chamaeleo parsoni crucifer*, 17 S, 70 G ex Madagascar, Perinet, 1 N. (Paris, I. Landau).

    robinsoni: *Chamaeleo brevicornis*, 50 G, ex Madagascar, Sous-Pref. Moramanga, Fiherenana, 1 N, TYPE (Paris, I. Landau).

CARINAMOEBA

11.	*minasense anolisi*:	*Anolis limifrons*, 56 S, 75 G ex Panama, Canal Zone, 4.8 km N Gamboa, Frijolito Cr., 3 N, TYPE; San Blas Terr., 5 km W Mulatupo, Sasardi, 2 N.
12.	*minasense capitoi*:	*Anolis capito*, 50 S, 50 G ex Panama, Canal Zone, 4.8 km N Gamboa, Frijolite Cr., 2 N, TYPE.
	minasense carinii:	*Iguana iguana*, 25 S, 3 G, ex Colombia, Barranquillo (?) vicinity, 1 N.
13.	*minasense diminutivum*:	*Ameiva ameiva*, 50 S, 22 G, ex Panama, Colon Prov., Guayabalito village on Chagres R., 1 N, TYPE; Canal Zone, Madden Dam, 1 N; Panama Prov., Santa Rita Chorrera, 1 N.
14.	*minasense plicae*:	*Plica umbra*, 25 S, 25 G ex Guyana, Georgetown vic., 1 N, TYPE.
15.	*minasense tegui*:	*Tupinambis teguixin*, 50 S, 50 G, 1 N & 1 E ex Venezuela, Est. Portuguesa, Mun. Piritú, San Jorge, TYPE.
16.	*minasense* ssp indet.:	*Anolis distichus*, 50 S, 50 G, ex Dominican Republic, R. Seibo at Pedro Sanchez, 1 N.
17.	*minasense* ssp indet.:	*Anolis cybotes*, 75 S. 75 G, ex Dominican Republic, R. Seibo at Pedro Sanchez, 1 N; Morro de Michel, 1 N.
18.	*marginatum*:	*Anolis frenatus*, 99 S, 75 G, ex Panama, Canal Zone, 4.8 km N Gamboa, Frijolito Cr., 1 N, TYPE; Canal Zone, 4.8 km N Gamboa, Quebrada Juan Grande, 1 N; Canal Zone, Barro Colorado I., 1 N; Panama Prov., El Aguacate, 1 N.
19.	*rhadinurum*:	*Iguana iguana*, 75 S, 34 G, ex Mexico, Est. Colima, 1 N; Venezuela, Est. Portuguesa, Mun. Guanare, Fundo Vega Honda, 1 N.
20.	*attenuatum*:	*Ameiva ameiva*, 60 S, 46 G, ex Guyana, Georgetown vic., 1 E, TYPE; Venezuela, Est. Portuguesa, Mun, Piritú, San Jorge, 2 N; Est. Cojedes, Mun. Manrique, Tierra Caliente, 1 N.
21.	*scelopori*:	*Sceloporus teapensis*, 40 S, 75 G, ex Belize, 16 km N Augustine, Blancaneaux Lodge, 2 N, TYPE.
	scelopori:	*Sceloporus variabilis*, 50 G, Honduras, 2 N.
22.	*mabuiae*:	Mabuya maculilabris, 19 S, 24 G, ex Lwiro, Kivu Prov., Zaire, 1 N.
23.	*mabuiae*:	*Mabuya striata*, 75 S, 100 G, ex Tanzania, Morogoro Reg., Morogoro, 4 N; 25 G ex Kenya, Nairobi, 1 N. (London, P.C.C. Garnham).

24. *Plasmodium cordyli*: *Cordylus cordylus tropidosternum*, 90 S, 50 G, ex Tanzania, Tanga Reg., E. Usambara Mtns, Magrotto Mtn, 1 N; Lindi Reg., Rondo Plateau, 3.8 km W Rondo Forestry Sta., 1 N.

LACERTAMOEBA

26. *tropiduri tropiduri*: *Tropidurus torquatus*, 43 S, 50 G, ex Guyana, Georgetown vicinity, 1 N.

27. *tropiduri tropiduri*: *Tropidurus hispidus*, 75 S, 131 G, ex Venezuela, Estado Portuguesa, Mun. Araure, Araure, 1 N; Estado Portuguesa, Mun. Guanare, Fundo Vega Honda, 4 N; Estado Guarico, Bancos de su Pedro, 1 N.

28. *tropiduri panamense*: *Anolis biporcatus*, 161 S, 154 G, ex Panama, Panama Prov., El Aguacate, 8 N, TYPE.

29. *tropiduri aquaticum*: *Anolis lionotus*, 120 S, 103 G, ex Panama, Colon Prov., 4.8 km SE Achiote village, 3 N, TYPE; Panama, Panama Prov., El Aguacate, 2 N.

30. *tropiduri aquaticum*: *Anolis poecilopus*, 84 S, 83 G, ex Panama, Panama Prov., Gaspar Sabana-Madrono, 3 N; Panama, Canal Zone, 4.8 km N Gamboa, Frijoles R.-Frijolito Cr., 2 N.

31. *tropiduri* ssp. indet.: *Anolis pentaprion*, 10 S, 50 G, ex Panama, Panama Prov., El Aguacate, 2 N.

32. *tropiduri* ssp. indet.: *Anolis cybotes*, 88 S, 150 G, ex Dominican Republic, Rio Seibo at Pedro Morales, 4 N.

33. *floridense*: *Sceloporus undulatus*, 163 S, 210 G, ex Florida, Alachua Co., Gainesville, 2 N; Georgia, Baker Co., 1 N. (C.G. Huff); Georgia, Clinch Co., 4.8 km NW Edith, 1 N (D.G. Young); Georgia, 2 E. (G.H. Ball).

34. *floridense*: *Sceloporus woodi*, 25 S, 25 G, ex Florida, Alachua Co., Gainesville, 1 E.

35. *floridense*: *Anolis carolinensis*, 375 S, 361 G, ex Florida, Alachua Co., Gainesville, 2 N, 1 E; Florida, Marion Co., Oklawaha R. at Eureka, 1 N; Florida, Gilchrist Co., Hart Springs, 1 N; Florida, Dade Co., Miami, 1 N; Florida, Collier Co., Collier-Seminole State Park, 1 N; Florida, Lee Co., Pine Island, 1 N; Florida, DeSoto Co., Hwy. 61 nr. Horse Cr., 1 N, 1 E; Georgia, Baker Co., 1 E (C.G. Huff); Georgia, 1 E (G.H. Ball).

36. *floridense*: *Anolis sagrei*, 23 S, 25 G ex Bahama I., N. Bimini, 1 N.

37. *floridense*: *Sceloporus malachiticus*, 21 S, 40 G, ex Panama, Chiriqui Prov., El Volcan, 1 N (C.G. Huff).

38. *floridense*: *Anolis limifrons*, 245 S, 328 G, ex Panama, Canal Zone, 4.8 km SE Achiote village, 2 N; Panama, Canal Zone, 4.8 km N Gamboa, Frijolito Cr. & Quebrada Juan Grande, 3 N;

		Panama, Canal Zone, Madden Forest, 1 N; Panama, Darien Prov., Cerro Pirre, 1 N; Panama, San Blas Terr., 5 km W Mulatupo, Sasardi, 4 N.
39.	*floridense*:	*Anolis biporcatus*, 56 S, 100 G, ex Panama, Panama Prov., El Aguacate, 2 N; Panama, Canal Zone,Chiva Chiva, 1 N; Panama, Canal Zone, 4.8 km SE Achiote village, 1 N.
	floridense:	*Anolis pentaprion*, 25 S, ex Panama, Panama Prov., El Aguacate, 1 N.
	floridense:	*Anolis frenatus*, 20 S, ex Panama, Canal Zone, 4.8 km N Gamboa, 1 N.
40.	*floridense*:	*Anolis lemurinus*, 50 S, 50 G, ex Belize, Blancaneaux Lodge, 2 N.
41.	*floridense*:	*Anolis tropidonotus*, 75 S, 108 G, ex Mexico, Estado Veracruz, San Andres Tuxtlas, 2 N; Honduras, 2 N (A. Lowichik).
42.	*floridense*:	*Anolis conspersus*, 75 S, 66 G, ex Grand Cayman I., 3 N.
43.	*floridense*:	*Anolis distichus*, 51 S, 52 G, ex Dominican Republic, Trepoda de Jabilla, 1 N.
44.	*floridense*:	*Anolis cybotes*, 77 S, 100 G, ex Dominican Republic, Rio Seibo at Pedro Sanchez, 2 N; Haiti, Dept. de l'Ouest, N slope Massif de la Selle, Fond Verrettes, 2 N.
45.	*floridense*:	*Anolis pulchellus*, 50 S, 100 G, ex Puerto Rico, Rio Grande, 1 N, 1 E.
46.	*floridense*:	*Anolis garmani*, 58 S, 100 G, ex Jamaica, Worthy Park, 1 N; Jamaica, Somerset, 3 N.
	floridense:	*Anolis opalinus*, 50 G, ex Jamaica, Mandeville, 1 N.
47.	*floridense*:	*Anolis lineatopus*, 57 S, 100 G, ex Jamaica, Montego Bay, 1 N; Jamaica, Worthy Park, 2 N; Jamaica, Portland Cottage, 1 N; Jamaica, Somerset, 1 N.
48.	*Plasmodium uncinatum*:	*Plica plica*, 23 S, 29 G, ex Guyana, Georgetown vicinity, 1 N, TYPE.
49.	*Plasmodium colombiense*:	*Anolis auratus*, 75 S, 75 G ex Colombia, Cali vicinity, 1 N (S.C. Ayala); Venezuela, Estado Portuguesa, Mun. Guanare, Fundo Vega Honda, 1 N.
50.	*Plasmodium* sp. indet.:	*Anolis limifrons*, 45 S, 50 G, ex Panama, Canal Zone, 4.8 km N Gamboa, Frijolito Cr. & Pipeline Road, 2 N.
51.	*Plasmodium* sp. indet.:	*Anolis distichus*, 25 S, 52 G, ex Dominican Republic, Rio Seibo at Pedro Sanchez,1 N.
52.	*Plasmodium brumpti*:	*Sceloporus horridus*, 23 S, 25 G ex Mexico, Estado Morelos, Coatetelco, 1 N (D. Pelaez).

53. *Plasmodium vacuolatum*: *Plica umbra*, 25 S, 25 G, ex Guyana, Georgetown vicinity, 1 N.

54. *Plasmodium iguanae*: *Iguana iguana*, 49 S, 25 G, ex Venezuela, Estado Portuguesa, Mun. Guanare, Fundo Vega Honda, 1 N, TYPE.

55. *Plasmodium basilisci*: *Basiliscus basiliscus*, 100 S, 50 G, ex Panama, Colon Prov., Achiote village, 1 N; Panama, Canal Zone, Madden Forest, 1 N; Panama, Panama Prov., El Augacate, 1 N.; Panama, San Blas Terr., 5 km W Mulatupo, Sasardi, 1 N.

56. *Plasmodium telfordi*: *Ameiva ameiva*, 72 S, 129 G, ex Guyana, Georgetown Vicinity, 1 E; Venezuela, Estado Portuguesa, Mun. Araure, Hoja Blanca, 1 N; Venezuela, Estado Portuguesa, Mun. Piritu, San Jorge, 1 N.

57. *Plasmodium aurulentum*: *Thecadactylus rapicauda*, 84 S, 105 G, ex Panama, Canal Zone, Madden Dam, 2 N TYPE; Panama, San Blas Terr., 5 km W Mulatupo, Sasardi, 2 N; Venezuela, Estado Portuguesa, Mun. Manrique, Tierra Caliente, 1 N.

58. *Plasmodium beebei*: *Gonatodes taniae*, 50 S, 50 G, ex Venezuela, Estado Aragua, Parque Nacional Henri Pittier below Rancho Grande, 1 N, TYPE.

59. *Plasmodium sasai*: *Takydromus tachydromoides*, 490 S, 426 G, ex Japan, Honshu, Niigata Pref., Mt. Yahiko, 1 N; Japan, Honshu, Saitama Pref., Hanno, 2 N, 5 E, TYPE.

60. *Plasmodium sasai*: *Takydromus smaragdinus*, 33 S, 75 G ex Japan, Ryukyu I., Amami Oshima, Koniya, 2 N, 1 E.

61. *Plasmodium sasai*: *Takydromus sexlineatus*, 50 S, 75 G ex Thailand, Ramintra, nr. Bangkok, 2 N.

62. *Plasmodium mackerrasae*: *Egernia whitei*, ex Australia, So. Queensland, 48 S, 53 G, 1 E, TYPE.

Plasmodium mackerrasae: *Egernia cunninghami*, Australia, So. Queensland, 1 N.

63. *Plasmodium agamae*: *Agama agama*, 240 S, 500 G, ex Zaire, 12 km WSW Kinsuka, on Congo R., 1 N; Zaire, Equateur Prov., Sub-Ubangui, Gemena, 2 N.

64. *Plasmodium agamae*: *Agama agama*, ex Tanzania, Morogoro Region, Nguru Mtns, Mkindo R. above Mkindo village, 1 N; Tanzania, Morogoro Region, Nguru Mtns, Mahuvuge R. x3 km SW Turiani, 1 N.

65. *Plasmodium agamae*: *Agama agama*, ex Sierra Leone, Freetown, 1 N; Nigeria, 3 N (P.C.C. Garnham).

66. *Plasmodium agamae*: *Agama mossambica*, 84 S, 175 G, ex Tanzania, Morogoro Region, Morogoro, N slope Uluguru Mtns at Univ.

		Campus, 3 N; Tanzania, Tanga Region, E. Usambara Mtns, below Amani, 1 N.
67.	*Plasmodium holaspi*:	*Holaspis guentheri*, 67 S, 85 G, ex Tanzania, Morogoro Region, S Side Uluguru Mtns, Kimboza Forest, 2 N, TYPE.
68.	*Plasmodium pitmani*:	*Mabuya striata*, 150 S, 176 G, ex Kenya, Nairobi, 1 N; Kenya, Kodera Forest, 1 N; Tanzania, Morogoro Region, Morogoro, 1 N.
	Plasmodium pitmani:	*Mabuya varia*, 50 G, ex Tanzania, Morogoro Region, Morogoro, N slope Uluguru Mtns.
	Plasmodium pitmani:	*Mabuya maculilabris*, 32 G, ex Zaire; Kinshasa, 1 N.
69.	*Plasmodium michikoa*:	*Chamaeleo tenuis*, 75 S, 100 G, ex Tanzania, Morogoro Region, E Uzungwe Mtns, Sanje, 1 N.
70.	*Plasmodium gologoloense*:	*Chamaeleo tenuis*, 54 S, 75 G, ex Tanzania, Morogoro Region, E Uzungwe Mtns, Sanje, 1 N.
71.	*Plasmodium tanzaniae*:	*Chamaeleo werneri*, 57 S, 125 G, ex Tanzania, Iringa Region, W Uzungwe Mtns, Mufindi, 3 N.
72.	*Plasmodium uzungwiense*:	*Chamaeleo werneri*, 50 S, 110 G, ex Tanzania, Iringa Region, W Uzungwe Mtns, Mufindi, 1 N.
73.	*Plasmodium arachniformis*:	*Chamaeleo werneri*, 125 S, 200 G, ex Tanzania, Iringa Region, W Uzungwe Mtns, Mufindi, 3 N, 1 E.
74.	*Plasmodium zonuriae*:	*Cordylus vittifer*, 105 S, 125 G. ex South Africa, SW Transvaal, Potchefstroom Dist., 2 N; South Africa, Transvaal, Die Berg, 1 N; South Africa, Transvaal, Pretoria, 1 N.
75.	*Plasmodium zonuriae*:	*Pseudocordylus microlepidotus*, 25 S, 50 G, ex SE Africa, 1 N.
76.	*Plasmodium loveridgei*:	Lygodactylus picturatus, 215 S, 275 G, ex Tanzania, Morogoro Region, Morogoro, N slope Uluguru Mtns at Univ. Campus, 6 N, TYPE.
77.	*Plasmodium loveridgei*:	*Lygodactylus grotei*, 75 S, 75 G ex Tanzania, Morogoro Region, Morogoro, N slope Uluguru Mtns at Univ. Campus, 2 N, 1 E.
78.	*Plasmodium cnemaspi*:	*Cnemaspis africana*, 100 S, 175 G, ex Tanzania, Morogoro Region, S side Uluguru Mtns, Kimboza Forest, 5 N, TYPE.
79.	*Plasmodium uluguruense*:	*Hemidactylus platycephalus*, 135 S, 150 G, ex Tanzania, Morogoro Region, Morogoro, N slope Uluguru Mtns, 2 N, TYPE; Tanzania, Morogoro Region, S side Uluguru Mtns, Kimboza Forest, 2 N; Tanzania, Morogoro Region, Morogoro, Mindu Mtn, 1 N.

Plasmodium maculilabre: *Mabuya maculilabris*, 20 G, ex Zaire, Kisangani, 1 N. (W. Verheyen).

80. *Plasmodium brygooi*: *Chamaeleo brevicornis*, 17 S, 48 G, ex Madagascar, 1 N (Paris, I. Landau).

81. *Plasmodium cordyli* ssp. ?: *Cordylus vittifer*, 25 S, 50 G, ex South Africa, Transvaal, Pretoria, 1 N; Transvaal, Middleburg, 1 N.

PARAPLASMODIUM

82. *Plasmodium mexicanum*: *Sceloporus torquatus*, 36 S, 100 G, ex Mexico, D.F., 1 N. (D. Pelaez); Mexico, Estado Mexico, 8.4 km E turnoff to Via Victoria on Hwy 15, 1 N.

83. *Plasmodium mexicanum*: *Sceloporus occidentalis*, 100 S, 125 G, ex California, Mendocino Co., Hopland Field Sta., 1 N; California, Mendocino Co., Hopland Valley, 1 N; Sacramento Co., 29.0 km E, Sacramento, 2 N; California, San Francisco Bay area, 1 E (G.H. Ball).

84. *Plasmodium chiricahuae*: *Sceloporus jarrovii*, 70 S, 310 G, ex Arizona, Cochise Co., Chiricahua Mtns, 2.9 km above Onion Saddle, 2 N, TYPE; Arizona, Cochise Co., Chiricahua Mtns, above American Museum of Natural History Field Station, 1 N; Arizona, Graham Co., Pinaleno Mtns, 1 N.

85. *Plasmodium chiricahuae*: *Sceloporus poinsetti*, 6 S, 150 G, ex Texas, Llano Co., Enchanted Rock, 4 N.

Plasmodium chiricahuae: *Urosaurus ornatus*, 1 S, 25 G, ex Texas, Llano Co., Enchanted Rock, 1 N.

ASIAMOEBA

86. *Plasmodium saurocaudatum*: *Mabuya multifasciata*, 25 S, 301 G, ex Singapore, MacRitchie Reservoir, 1 N, TYPE; Southern Thailand, 4 N.

87. *Plasmodium lionatum*: *Ptychozoon lionatum*, 50 S, 100 G, ex Southern Thailand, 2 N, TYPE.

88. *Plasmodium* sp. indet.: *Varanus grayi*, 57 S, 21 G, ex Philippines, Luzon, Caramoan Penin., Caramoan Mun., Caputatan, 2 N (W. Auffenberg).

GARNIA

Plasmodium gonatodi: *Gonatodes fuscus*, 75 S, 125 G, ex Panama, San Blas Terr., 5 km W Mulatupo, Sasardi, 5 N, TYPE.

Plasmodium morulum: *Mabuya mabouya*, 95 S, 100 G, ex Panama, San Blas Terr., 5 km W Mulatupo, Sasardi, 1 N, 1 E, TYPE.

Plasmodium lainsoni:	*Phyllodactylus ventralis*, 46 S, 100 G, ex Venezuela, Estado Portuguesa, Mun. Guanare, Fundo Vega Honda, 1 N, TYPE.
Plasmodium scorzai:	*Phyllodactylus ventralis*, 69 S, 101 G, ex Venezuela, Estado Portuguesa, Mun. Guanare, Fundo Vega Honda, 4 N, TYPE.
Plasmodium balli:	*Anolis lionotus*, 72 S, 151 G, ex Panama, Colon Prov., 4.8 km SE Achiote village, 3 N, TYPE; Panama, Panama Prov., El Aguacate, 3 N.
Plasmodium balli:	*Anolis poecilopus*, 82 S, 229 G, ex Panama, Canal Zone, 4.8 km N Gamboa, Frijolito Cr. & Quebrada Juan Grande, 4 N; Panama, Panama Prov., Gaspar Sabana, 1 N.
Plasmodium balli:	*Anolis limifrons*, 59 S, 150 G, ex Panama, Canal Zone, 4.8 km SE Achiote village, 1 N; Panama, Canal Zone, Madden Forest, 1 N; Panama, Canal Zone, 4.8 km N Gamboa, Frijolito Cr. & Quebrada Juan Grande, 2 N; Panama, San Blas Terr., 5 km W Mulatupo, Sasardi, 1 N.
Plasmodium azurophilum:	*Anolis cybotes*, 126 S, 135 G, ex Haiti, Dept. de l'Ouest, N slope Massif de La Selle, Fond Verretes, 3 N, TYPE; Haiti, Petionville, 1 N; Dominican Republic, Rio Seibo at Pedro Sanchez, 1 N.
Plasmodium azurophilum:	*Anolis armouri*, 26 S, 50 G. 2 E, ex *A. cybotes*.
Plasmodium azurophilum:	*Anolis krugi*, 22 S, 50 G, ex Puerto Rico, 1 N.
Plasmodium azurophilum:	*Anolis lineatopus*, 28 S, 45 G, ex Jamaica, Montego Bay, 2 N.
Plasmodium azurophilum:	*Anolis grahami*, 3 S, 10 G ex Jamaica, Montego Bay, 1 N.

OPHIDIELLA

Plasmodium tomodoni:	*Tomodon dorsatus*, 25 S, 25 G, ex Brazil, Estado Sao Paulo, Cananeia, 1 N (S. B. Pessoa).

FALLISIA

simplex:	*Plica umbra*,25 S, 25G, ex Guyana, Georgetown vicinity, 1 N.
siamense:	*Draco maculata*, 25 S, 50 G, ex Thailand, Bangkok, nr. Ramintra, 1 N, TYPE.
sp. indet.:	*Anolis cybotes*, 8 S, 30 G, ex Dominican Republic, Rio Seibo at Pedro Sanchez, 1 N.

SAUROCYTOZOON

tupinambi: *Tupinambis teguixin*, 25 G, ex Venezuela, Estado Portuguesa, Municipio Piritu, San Jorge, 1 N.

mabuyi: *Mabuya multifasciata*, 156 G, ex Singapore, MacRitchie Reservoir, 1 N; Southern Thailand, 6 N.

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